Caribbean Journal of Science, Vol. 44, No. 3, 279-286, 2008

Miocene sharks in the Kendeace and Grand Bay formations of Carriacou, The Grenadines, Lesser Antilles

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ABSTRACT.—The Miocene chondrichthyan fauna from the Kendeace and Grand Bay formations consists of five species which have been identified from the remains of teeth. These are *Carcharias taurus* (sand-tiger shark), *Isurus oxyrinchus* (shortfin mako shark), *Carcharocles megalodon* (mega-tooth shark), *Carcharhinus obscurus* (requiem shark) and *Hemipristis serra* (extinct snaggletooth shark). No further skeletal fish remains, Chondrichthyes or Actinopterygii, were discovered. Teeth of *Carcharhinus obscurus* predominated, by greater than three to one, the other shark species found in these deposits.

KEYWORDS.—Caribbean, Neogene, Chondrichthyes, volcaniclastics.

INTRODUCTION

Despite our knowledge from focused research campaigns and considerable general interest, the fossil record of vertebrates from the Antillean region remains patchy, somewhat biased in its scope and, thus, is rather incomplete. The bias is not due to selective collection so much as the sporadic patterns of preservation across the region. Terrestrial vertebrates are mainly known from Quaternary deposits where bone-rich cave sediments continue to provide a bonanza for the collector (e.g., Morgan, 1993; McFarlane and Blake, 2005); although many, perhaps most of these are no older than the last interglacial (MacPhee et al., 1989). Pre-Quaternary terrestrial vertebrates remain elusive (reviewed in Portell et al., 2001: 191-192). Thus, our knowledge of the terrestrial tetrapods of the region is strongly biased towards the youngest part of the fossil record, and thus fails to provide a true document of their evolution and biogeography in the Antilles.

It might be predicted that the ancient Antillean fishes would have a less polarized fossil record as marine sedimentary deposits are particularly widespread throughout the region. While this is undoubtedly true, some deposits appear to be peculiarly depauperate in fish remains (Purdy et al., 1996); articulated skeletons of fossil fishes are unknown and identifications are consequently based on the identification of isolated skeletal elements such as otoliths (e.g., Nolf, 1976; Nolf and Stringer, 1992; Nolf and Aguilera, 1997; Stringer, 1998) and teeth (e.g., Casier, 1958; Iturralde-Vinent et al., 1996; Flemming and McFarlane, 1998; Underwood and Mitchell, 2000; Donovan and Gunter, 2002). Thus, the fossil record of Antillean fishes is much superior to that of tetrapods, providing more and better pre-Quaternary specimens and species, and having a wider geographic distribution, albeit based upon taxa with easily preservable teeth (e.g., sharks) or otoliths (teleosts). Accordingly, the region provides great potential for the discovery and description of new faunas.

Herein, we document such a new fauna of sharks' teeth from the Miocene of Carriacou, The Grenadines. These were first mentioned by RWP in Donovan et al. (2003: 265). The occurrence of these teeth is disparate, collected during three field trips to the island. The moderate diversity represents the result of many hundreds of man-hours of collecting by RWP, SKD, RKP, and DATH, indicating their rarity compared with, for example, associated fossil mollusks (Jung, 1971).

Except as noted, all shark teeth discussed herein are catalogued into the Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, and are identified by the prefix UF followed by the catalogue number. Fossil localities referred to throughout the paper and in Figure 1 were designated by the Invertebrate Paleontology Division, Florida Museum of Natural History and are denoted by the prefix FLMNH IP followed by a letter and number designation.

Geological Setting

Donovan et al. (2003: 257-258) provided an overview of the geology of Carriacou. The Miocene sedimentary succession consists of the Belmont, Kendeace, Carriacou and Grand Bay formations (Fig. 1). The lower to middle Miocene Kendeace Formation is discontinuous, but mappable, and has a maximum thickness of about 40 m (Speed et al., 1993). It consists of volcaniclastic sandstones with some more carbonate-rich horizons. The contact with the underlying Belmont Formation is unconformable; the Kendeace Formation grades upwards into the carbonate-rich Carriacou Formation.

The middle Miocene Grand Bay Formation is a volcaniclastic turbidite succession deposited in a more easterly basin to the other Miocene formations and at a water depth in excess of 150 m (Donovan et al., 2003). The deepwater origin is demonstrated by abundant sedimentological, paleontological, and ichnological features. Body fossils includes terrestrial, benthic, nektic and planktic mollusks, scleractinian corals, terebratulide brachiopods, echinoids, crinoids, asteroids, decapod crustaceans, and barnacles. This assemblage, obviously disharmonious, include both autochthonous/parautochthonous (e.g., brachiopods and crinoids) and allochthonous taxa, such as terrestrial gastropods and shallow-water, colonial scleractinians.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES

Order Lamniformes

Family ODONTASIPIDIDAE (sand tiger sharks)

Genus Carcharias *Rafinesque, 1810*

Carcharias taurus Rafinesque, 1810

Material examined, locality, and age.—Three teeth, UF 217703 (Fig. 2A, B), UF 217717 and UF 217718. All specimens were derived from FLMNH IP locality XU004, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Series E803 (1978), GPS 12.475512, −61.432364 (datum WGS 84); middle Miocene Grand Bay Formation (see Fig. 1).

Description.—UF 217703, the most complete tooth of this species, is a lower anterior tooth, and, as preserved, has a maximum width of 7.8 mm, maximum height of 21.0 mm and maximum thickness of 4.8 mm. The crown is smooth-sided, but pits sporadically occur on both the smooth lingual (inner) and labial (outer) surfaces. No lateral cusplets or root remains. The crown flattens and thickens nearest the absent root, and curves upward near the tip but then flattens at the end. UF 217718 is less complete and consists of an incomplete crown with morphology similar to the aforementioned specimen. However, no pitting is present on the crown surface. Maximum width of UF 217718 is 7.5 mm, maximum height is 21.4 mm, and maximum thickness is 4.9 mm. UF 217717 lacks both the root and much of the crown.

Discussion.—This large and bulky shark grows to a length of 3.18 m, and is a voracious feeder on bony fishes, small sharks, rays, arthropods and cephalopods. *Carcharias taurus* is littoral and its range is very limited, usually occurring at or near the bottom on the outer shelves in surf zones, shallow bays and coral and rocky reefs (Compagno, 1984).

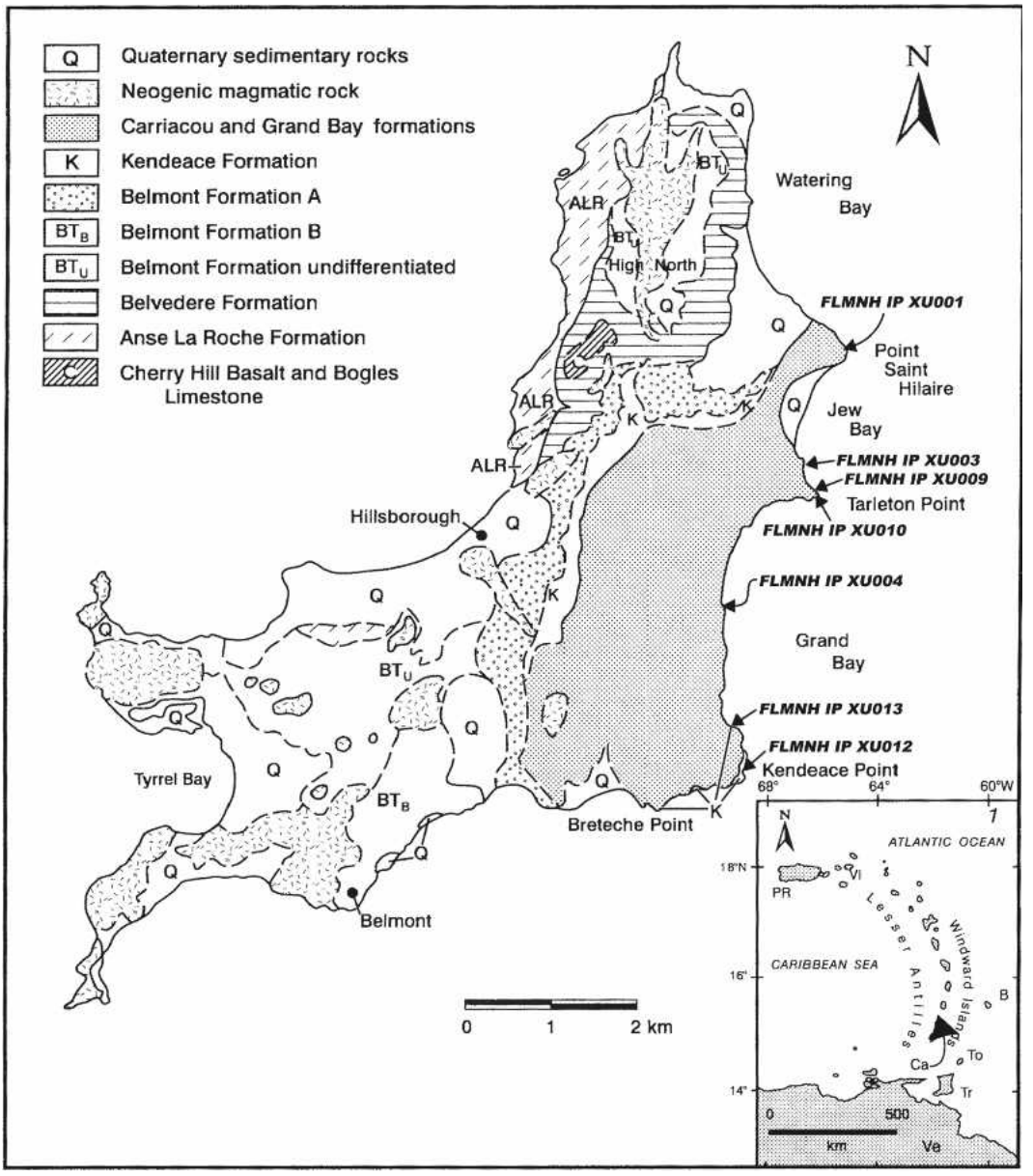

FIG. 1. Modified geological map of Carriacou (after Donovan et al., 2003: fig. 1). Inset map of Lesser Antillean region shows the position of Carriacou (arrowed). Key: B = Barbados; Ca = Carriacou; PR = Puerto Rico; To = Tobago; Tr = Trinidad; Ve = Venezuela; VI = Virgin Islands. The five Grand Bay Formation (FLMNH IP XU001, XU003, XU004, XU009, and XU010) and two Kendeace Formation (FLMNH IP XU012 and XU013) shark tooth collecting localities are also denoted.

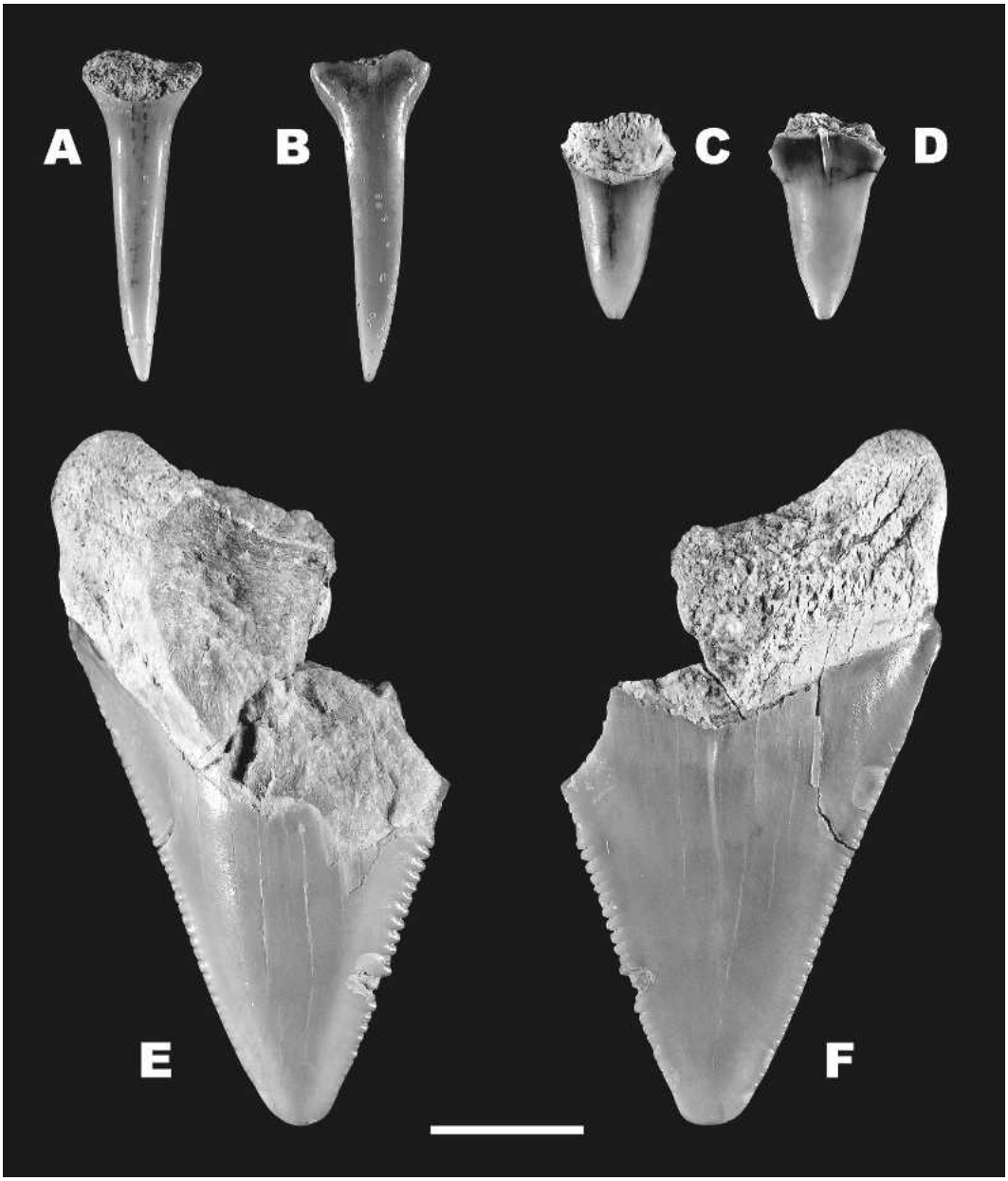

FIG. 2. Fossil *Carcharias*, *Isurus*, and *Carcharocles* teeth from the Miocene Kendeace and Grand Bay formations. A-B, *Carcharias taurus* Rafinesque, UF 217703. A. Lingual view. B. Labial view. C-D, *Isurus oxyrinchus* Rafinesque, UF 217702. C. Lingual view. D. Labial view. E-F, *Carcharocles megalodon* (Agassiz), RGM 283 399. E. Lingual view. F. Labial view. Scale bar represents 10 mm.

Family LAMNIDAE (mackerel, mako and white sharks)

Genus Isurus *Rafinesque, 1810*

Isurus oxyrinchus Rafinesque, 1810

Material examined, locality, and age.—Six teeth, UF 217702 (Fig. 2C, D) and UF 217712-217716. Of these, UF 217713-UF 217715 were derived from FLMNH IP locality XU004, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Series E803 (1978), GPS 12.475512, −61.432364 (datum WGS 84); middle Miocene Grand Bay Formation; UF 217716 was collected at FLMNH IP locality XU009, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Series E803 (1978), GPS 12.487568, −61.42344 (datum WGS 84); middle Miocene Grand Bay Formation; and UF 217701 was excavated from FLMNH IP locality XU012, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Series E803 (1978), GPS 12.460117, −61.429971 (datum WGS 84); lower to middle Miocene Kendeace Formation.

Description.—UF 217702 is a lateral tooth with a maximum width of 6.6 mm, maximum height of 13.5 mm, and maximum thickness of 3.7 mm. This smooth-edged tooth has a partial root, attached only to the lingual surface which is smooth and convex. The smooth labial surface is flattened with the tip slightly down-turned. The five additional teeth of this species are smaller and/or less complete, consisting mostly of rootless crowns.

Discussion.—This is an offshore littoral and epipelagic species that grows to 3.94 m. *Isurus oxyrinchus* has a worldwide distribution in warm temperate and tropical seas, and usually preys on bony fishes, other sharks and cephalopods (Compagno, 1984).

Family OTODONTIDAE (mega-toothed sharks)

Genus Carcharocles *Jordan and Hannibal, 1923*

Carcharocles megalodon (Agassiz, 1843)

Material examined, locality, and age.—The single tooth (Fig. 2E, F) reposited in the Nationaal Natuurhistorisch Museum, Leiden, as RGM 283 399, was collected at FLMNH locality XU013, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Series E803 (1978), GPS 12.463584, −61.430372 (datum WGS 84); lower to middle Miocene Kendeace Formation.

Description.—RGM 283 399 is a worn lower lateral tooth of a juvenile shark. As preserved, the maximum width is 24.5 mm, maximum height is 45 mm and maximum thickness is 10 mm. The triangular crown is well-preserved (where present), but less than half of the U-shaped root remains. The more complete (left) margin is finely serrated with approximately 50 serrae. The labial surface is relatively flat and the lingual surface is convex with the thickest portion nearest the root.

Discussion.—*Carcharocles megalodon* is the largest macro-predatory shark that lived. This species ranged from the Miocene to the early Pliocene. Size estimates of this shark can only be extrapolated from fossil teeth and vertebrae. Maximum length of this species is estimated at 17 m, with a body mass of more than 65.6 tons (59,413 kg). Females are assumed to have grown much larger than males, a condition seen in Recent *Carcharodon carcharias* (white shark). Bite marks on fossil bones indicate that *C. megalodon* preyed mainly on cetaceans, pinnipeds and other large marine vertebrates. Fossils of this species have been found in North and South America, the Caribbean, Europe, Africa, Japan and Australasia, and occur mainly in nearshore deposits at subtropical to moderately high-temperate latitudes. This supports the speculation that *C. megalodon* favored biologically rich, nearshore and coastal shelf regions, similar to *C. carcharias*. These environments would have supported the large prey of this mega-tooth shark (Gottfried et al., 1996).

Order Carcharhiniformes
Family CARCHARHINIDAE (requiem sharks)

Genus Carcharhinus *de Blainville, 1816*

Carcharhinus obscurus (Lesueur, 1818)

Material examined, locality, and age.—Nineteen teeth, UF 217704-UF 217706 (Fig. 3A-F), UF 217707, UF 217708, UF 217719-

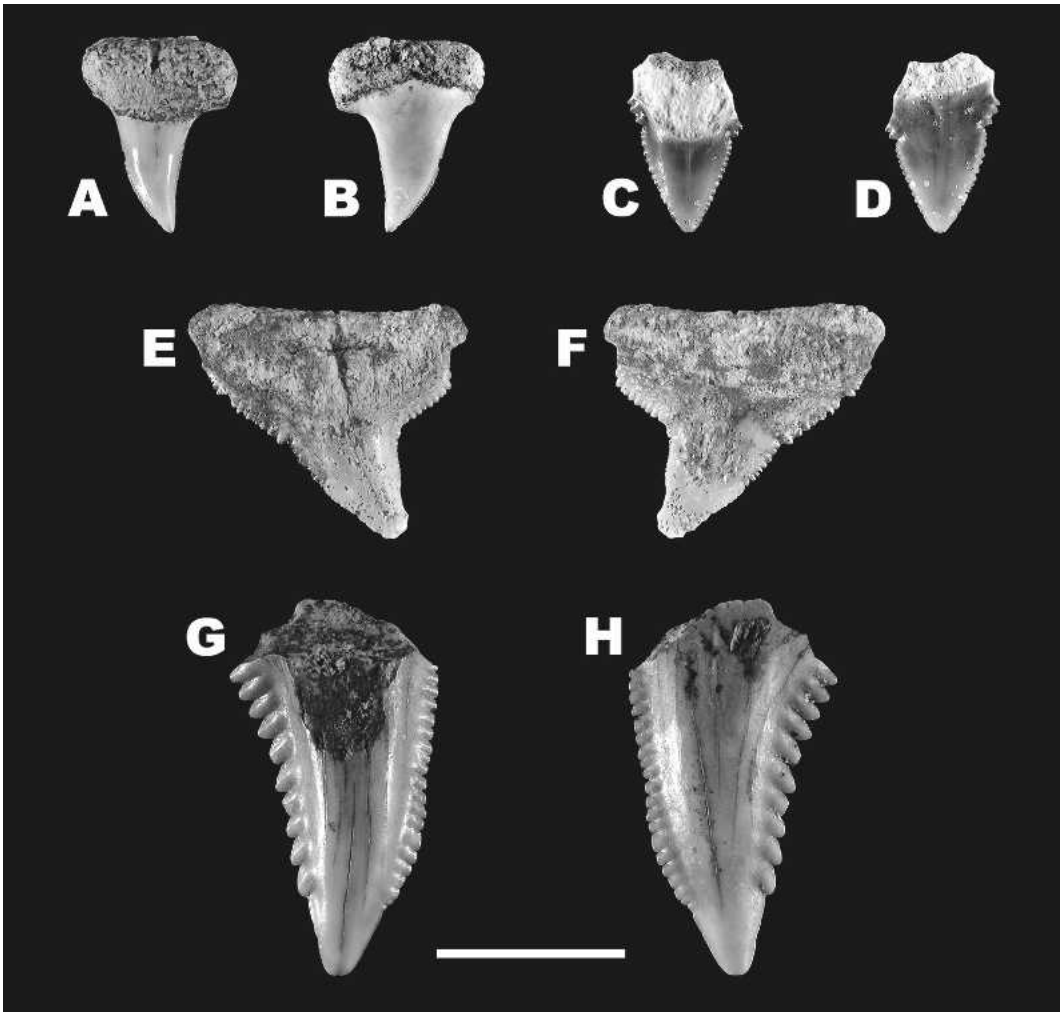

FIG. 3. Fossil *Carcharhinus* and *Hemipristis* teeth from the Miocene Kendeace and Grand Bay formations. A-F, *Carcharhinus obscurus* (Lesueur). A-B, UF 217704. A. Lingual view. B. Labial view. C-D, UF 217705. C. Lingual view. D. Labial view. E-F, UF 217706. E. Lingual view. F. Labial view. G-H, *Hemipristis serra* Agassiz, UF 217701. G. Lingual view. H. Labial view. Scale bar represents 10 mm.

UF 217722 and UF 217727-UF 217736. Of these, UF 217705 was collected from FLMNH IP locality XU001, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Series E803 (1978), GPS 12.503094, –61.422605 (datum WGS 84); middle Miocene Grand Bay Formation; UF 217708 was derived from FLMNH IP locality XU003, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Series E803 (1978), GPS 12.489823, –61.424637 (datum WGS 84); middle Miocene Grand Bay Formation; UF 217704 and UF 217729-UF 217735 were excavated from FLMNH IP locality XU004, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Series E803 (1978), GPS 12.475512, –61.432364 (datum WGS 84); middle Miocene Grand Bay Formation; UF 217719-UF 217721 were collected from FLMNH IP locality XU009, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Series E803 (1978), GPS 12.487568, –61.42344 (datum WGS 84); middle Miocene Grand Bay Formation; UF 217706, UF 217722, UF 217727, and UF 217728 were found at FLMNH IP locality XU010, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Se-

ries E803 (1978), GPS 12.486831, –61.422778 (datum WGS 84); middle Miocene Grand Bay Formation; and UF 217707 was derived from FLMNH IP locality XU013, Carriacou, Grenada (Grenadines). 1:25000 Sheet 5, Series E803 (1978), GPS 12.463584, –61.430372 (datum WGS 84); lower to middle Miocene Kendeace Formation.

Description.—UF 217704 is a nearly complete upper tooth with a finely serrated crown and negligible cusplets. The labial surface is convex and the lingual surface flat. As preserved, UF 217704 has a maximum width of 6.7 mm, maximum height of 8.8 mm and maximum thickness of 2.7 mm. UF 217705 is also a nearly complete tooth; however, both cusplets are more coarsely serrated than the rest of crown and the U-shaped root is missing its distal ends. UF 217705 has a maximum width of 6.0 mm, maximum height of 9.5 mm and maximum thickness of 2.6 mm. UF 217706 is a nearly complete upper right tooth and, like UF 217705, the serrae on the cusplets are coarser than on the main portion of the crown. The root is nearly complete but heavily worn. UF 217706 has a maximum width of 14.9 mm, maximum height of 12.4 mm and maximum thickness of 3.5 mm. The 16 additional teeth of this species are, for the most part, smaller and/or less complete, consisting mostly of rootless crowns of both upper and lower teeth.

Discussion.—*Carcharhinus obscurus* is a slender shark that grows to about 4 m and is found in the coastal-pelagic, inshore and offshore, warm-temperate and tropical waters of continental and insular shelves, and their adjacent oceanic waters. This species feeds on a wide variety of reef, bottom and pelagic bony fishes, other sharks, and also invertebrates, including arthropods, cephalopods, bryozoans and echinoderms (Compagno, 1984).

Family HEMIGALEIDAE (snaggletooth sharks)

Genus Hemipristis *Agassiz, 1843*

Hemipristis serra (Agassiz, 1843)

Material examined, locality, and age.—Three teeth, UF 217701 (Fig. 3G, H), UF 217710 and UF 217711. All were collected from FLMNH IP locality XU004, Carriacou, Grenada (Grenadines), 1:25000 Sheet 5, Series E803 (1978), GPS 12.475512, –61.432364 (datum WGS 84); middle Miocene Grand Bay Formation.

Description.—The most complete specimen of this species, UF 217701, is an upper anterior tooth, and, as preserved, has a maximum width of 10.7 mm, maximum height of 20.9 mm and maximum thickness of 4.5 mm. The crown is well-preserved, but no root remains. When viewed labially, margins along the crown are serrated with approximately ten coarse serrae on the left and 19 finer serrae on the right. Both the lingual and labial surfaces are moderately convex. UF 217710 is half (longitudinally) of an upper anterior tooth lacking its root while UF 217711 is a partial upper lateral, rootless tooth.

Discussion.—A now extinct species, *H. serra* had a worldwide distribution during the Miocene and Pliocene and has been reported from the Pleistocene. This shark has been most commonly found in neritic deposits containing warmwater faunas (Cappetta, 1987). Maximum body size, estimated from teeth, was probably close to 6 m. Diet was probably similar to its extant cousin *H. elongatus*, the only living species of this genus, and included bony fishes, sharks and rays. Due to its large size, *H. serra* probably would also have attacked larger prey (Kent, 1994).

Acknowledgments.—Fieldwork in Carriacou was supported by National Geographic Society research grants #5722-96 and #6625-99, which we gratefully acknowledge. Additional funding for fieldwork provided to R.W.P. by the FLMNH McGinty Endowment and to D.A.T.H. by the Carlsberg Foundation (Denmark). We thank Professor T. A. Jackson (University of the West Indies, Mona) and the late Dr. Roy Blackman for their assistance in the field. Sean Roberts (FLMNH) helped with digital photography. We thank Gary Stringer (University of Louisiana at Monroe) and an anonymous reviewer for helpful suggestions that improved the manuscript. This is

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